Journal of the Royal Society of Western Australia, 74, 1991, 115-127

Coral reefs in the Leeuwin Current - an ecological perspective

B G Hatcher

Oceanography Department, Dalhousie University, Halifax, Nova Scotia,B3H 4J1, Canada.

Abstract

The Leeuwin Current differs markedly from other eastern boundary currents in that it transports tropical water towards a polar ocean, and inhibits upwelling. As a result, the offshore marine environment of Western Australia is characterised by elevated sea temperatures and reduced dissolved nutrient and particulate concentrations relative to adjacent coastal and south-west Indian Ocean water masses. As in many western boundary currents, the distribution of coral reefs in and near the Leeuwin Current is extensive, and appears to mirror the influence of the current, with the limit of active reef accretion offshore extending well outside the tropics. Causality in the relationship between the regional oceanography and coral reef development has not been established, but the assumed dominance of sea temperature as a factor controlling reef growth is questioned on the basis of the evidence available. The Leeuwin Current's role in maintaining apparently low rates of nutrient delivery to the benthos, in combination with its elevation of sea temperature and advection of planktonic spores and larvae, serves to inhibit the development of marine macrophyte communities, which compete effectively with coral reef-building communities. At reefs where these two benthic community types overlap (*ie* the Houtman Abrolhos), periodic delivery of high nutrient water is inferred by the extent of non reef-building macrophyte communities. I suggest that the primary influence of the Leeuwin Current on coral reef development is to modulate the competition between coral and macrophyte communities. More oceanographic measurements, geological analyses and ecological experiments are required to test the hypothesis.

Introduction

The role of the Leeuwin Current in controlling the development and distribution of coral reefs along the Western Australian coast has been a subject of interest at least since Saville-Kent's (1897) observations of the Abrolhos reefs. There has also been a great deal of speculation on the topic, and precious little hard data collected. In this brief review I will make limited comparisons between the Leeuwin and other current systems, and discuss the most obvious mechanisms by which ocean currents may control reef growth. Finally, I will focus on the Abrolhos as the epitome of Leeuwin Current reefs.

Clear definition of terms is required. I have followed Fagerstrom (1987) in defining coral reefs as: "carbonate structures with a framework dominated by the skeletal remains of zooxanthellate, scleractinian corals, supporting a living veneer of those and other calcifying organisms". This definition encompasses the majority of photic zone, Holocene reefs, but specifically excludes aphotic zone reefs dominated by hermatypic corals, non-coral dominated reefs (*eg* algal-millepora reefs), and communities of corals living on non-coral reef structures such as limestone or sandstone.

The Leeuwin Current is well defined by Cresswell & Golding (1980), Thompson & Veronis (1982), Godfrey & Ridgway (1984), and by Pearce (1991) in this volume. It is a narrow (<200 km), shallow (<200 m) stream of relatively warm, low salinity, low nutrient oceanic water of tropical origin which flows southwards at relatively high velocity (0.1 - 0.4 ms^{-1}) along the western continental slope of Australia. The Current is driven by a latitudinal gradient of steric sealevel, is seasonal in its volume flux and sheds large and mesoscale eddies into the Indian Ocean and onto the shelf. The stream is coherent at least from North West Cape to Cape Leeuwin, with clear influence on flows on the Northwest Shelf and in the Great Australian Bight. I refer to this extent of continental shelf and slope as the "Leeuwin Province".

Coral Reef Initiation and Accretion

Extant coral reefs in the Leeuwin Province began growth within the past ten thousand years as coral communities recruiting to newly available marine substrata during the Holocene transgression. The basement could be either a former coral reef, killed during a glaciation perhaps, or any other hard surface in shallow water. Under suitable conditions reefs grew upwards at rates which approximated the rate of sealevel rise. Those which reached the sea surface then expanded horizontally.

Figure 1 Chart of the earth between the 40° parallels, showing the major boundary currents, the 18°C winter minimum monthly mean isotherm. and the distribution of coral reefs (modified from Neumann & Pierson 1966, Veron 1986). Boundary Current codes: A.C.= Agulhas Current, B.C.= Brazil Current (off S.America) & Benguela Current (off Africa), C.C.= California Current (off N.America) & Canary Current (off Africa), E.A.C.= East Australia Current, G.C.= Guiana Current (off S.America) & Guinea Current (off Africa), G.S.= Gulf Stream, K.S.C.= Kuro Shio Current, L.C.= Leeuwin Current, M.C.= Mozambique Current, P.C.= Peru Current (Humbolt Current). Latitudinal limits of coral reefs in the open ocean are indicated by doubled-ended brackets, those near coasts by single-ended brackets.

The essential dimension of reef growth is time. With upward accretion rates ranging from 1 to 10 mm per year, even modest reef structures represent temporal integration of environmental controls over thousands of years. Perhaps the single strongest message from oceanographic research during the last decade has been the variability of even the largest ocean structures. Rapid, glacially-forced change in sealevel is the penultimate control on patterns and rates of coral reef development (Davies & Montaggioni 1985). The ultimate control is the foundation upon which photic zone reefs must rest. Coral reefs cannot develop even under ideal atmospheric and seawater conditions if they have no structure within the upper 100 m of the ocean upon which to initiate growth.

The lack of shallow foundation is not a constraint on the shallower portions of the continental shelves off Western Australia, but is absolute on the shelf slope where the Leeuwin Current flows. The dearth of tectonism and related seamounts and guyots means that there are few potential reef sites actually in the Leeuwin Current: most are on the adjacent shelf or coast.

Even when the foundation of a Leeuwin reef is of coral construction, historical interruptions in vertical accretion of sufficient duration may have precluded subsequent reef development. The world's oceans are littered with the ghosts of drowned reefs, overlain by a photic zone ideal for coral growth (Menard 1986). Who knows what ghosts lie beneath the Leeuwin Current?

The process of reef accretion is the net result of a coral community's initiation and subsequent development in a particular environment. It requires:

1) A consistent supply of the larvae of reef-building, binding and infilling plants and invertebrates, most of which have a planktonic life stage. The supply can be from both local populations (*ie* self-seeding) and from distant reefs. Such immigration is a requisite for initial reef colonization.

2) Suitable substrata for larval settlement when they are delivered to a region: there must be available space on the seabed within the photic zone.

3) Suitable environmental conditions for the survival and growth of newly settled recruits through to the adult life stages, including:

   a) Non-lethal sea temperatures and salinities.

   b) Adequate irradiance for positive net daily photosynthesis by symbiotic and free-living algae.

   c) Adequate supplies of inorganic nutrients to meet the demands of autotrophic organisms for growth and calcification.

   d) Low concentrations of inorganic and organic particulates in the water column which otherwise inhibit coral growth by shading, smothering, and promoting bacterial infection.

Clearly many of the requirements for coral reef accretion such as temperature, light and nutrient concentration are the very factors which are strongly influenced by regional oceanography such as boundary currents. Poleward-flowing boundary currents, including the Leeuwin Current, have the potential to influence all of these factors, either directly or indirectly. The transport of tropical reef larvae and moderation of winter sea surface temperatures have received most attention. What can we learn about the Leeuwin's influence on coral reef development by looking at the global distribution of boundary currents and reefs?

Boundary Currents and Reef Systems

The global distribution of coral reefs as defined here is quite predictable (Fig.1). Reefs occur exclusively within the photic zone, and usually within 18°C mean monthly minimum isotherm. In the open oceans the latitudinal limits of reef development fall close to the tropics, generally within the 25th parallels (*eg* Midway in the north Pacific). Within semi-enclosed seas (*eg* Red Sea, Persian Gulf) and ocean margins however, the isotherms are distorted by continental influences and deflection of currents which close the great ocean circulations. Western boundary currents are the strongest, carrying warm water poleward in relatively narrow and deep streams such as the Mozambique - Agulhas Current system of eastern Africa. This current extends the poleward limit of reef development to well south of Durban (Fig.1).

On the eastern margins of the ocean basins the westerly flows of the major gyres are deflected towards the equator in slower boundary currents which are usually broad and shallow (Fig.1). Because of Coriolis' force and the trade winds, eastern boundary currents are generally characterized by upwelling at their coastal edges. Thus, the Benguela and Peru Currents are the analogs of the West Australian Current, and should serve as comparative models for the distribution of coral reefs in eastern boundary currents.

Such a comparison will perforce be brief. Only three reef systems (including the Galapagos) fall within the precinct of the Peru Current, the southernmost of which is at only 7°S near the coast at Chiclayo, Peru (Fig.1). All of them, including those at the Galapagos Islands over 1000 km from the South American coast, are marginal reefs in terms of their extent, diversity and vertical accretion rates. Coral reefs in the Gulf of Guinea at the northern extreme of the Benguela Current extend only 2°S of the equator.

It is apparent that the cold, nutrient-rich waters of eastern boundary currents somehow inhibit the development of coral reefs. Presumably, that is one reason why there are no open ocean atolls on the few seamounts in the West Australian Current. In contrast, the Elizabeth and Middleton Reefs occur at 29 to 30°S near Lord Howe in the East Australian Current.

The Leeuwin Current is clearly not a typical eastern boundary current. Its high poleward velocity and narrowness liken it to a western boundary current. But it is differently forced and shallower, so it moves a far smaller volume of water. In some ways it resembles the narrow currents which interpose between the major boundary currents and the coasts off North Africa and the America's, such as the Guinea Current and the Labrador Current extension. Both of these are equatorward currents, however, and are not strictly comparable with the Leeuwin.

As an oceanographic feature, the Leeuwin Current appears to be in a class by itself. The distribution of reefs along the Current, however, is repeated in poleward flowing boundary currents throughout the world. In terms of the factors controlling the development of coral reefs, more appropriate comparisons might be made with western boundary currents such as the Agulhas Current, the East Australian Current, the Kuro Shio Current and the Antilles/Florida/Gulf Stream current system. Like the Leeuwin Current, all of these sustain coral reefs in decreasing density and diversity along gradients through the tropics to well beyond them at Durban, Lord Howe Island, Kyushu Island and Bermuda respectively. They originate in regions rich in coral reefs and thus can transport reproductive propagules in a conducive biophysical regime.

Hydrologic Factors and Reef Growth

Space does not permit extending the comparisons in further detail here, but there is something to learn from examining parameters of reef structure and function along latitudinal gradients, and among boundary current systems. The major conclusion I draw is that while temperature alone is a reasonably good correlate of reef distribution, there are enough exceptions to the 18° 'law' (Wells 1957) at high latitude coral reefs to reject temperature as the sole factor limiting reef development.

The apparent correlation of coral reef distribution with minimum ocean temperatures (Fig.1) has led to the assumption of causality (Dana 1843, Rosen 1971, Burns 1985). The physiological data for individual coral species is far from conclusive. Corals and algae exhibit a high degree of plasticity in their responses to temperature extremes (reviewed in Brown & Howard 1985, Hatcher *et al.* 1989), and extrapolations from species-specific responses of local populations to reef building communities is problematical. Certainly instances of extensive natural mortality resulting from thermal stress have been documented (*eg* Shinn 1976, Roberts *et al.* 1982, Burns 1985), but active reef growth has been documented in environments where minimum mean temperatures extend well below 18°C (*eg* Downing 1985, Tribble & Randall 1986, Coles & Fadlallah 1991), and some species of hermatypic corals survive in temperatures as low as 11°C (*eg* MacIntyre & Pilkey 1969, Veron & Marsh 1988).

Identification of causality in controls on reef growth is complicated by the correlation of temperature, salinity, irradiance, nutrient and particulate gradients along geographic axes such as latitude and proximity to shore. Gradients of increasingly unsuitable environmental conditions for reef growth are characterized by a decrease in coral abundance and diversity, and an increase in the abundance of macroalgae (particularly Phaeophytes) at higher latitudes and close to continental land masses

(Johannes *et al.* 1983a, Birkeland 1988, Coles 1988, Sheppard 1988). Studies of reefs in the middle of this transition (*ie* supporting both coral and macrophyte-dominated communities) have led to the conclusion that competition for space, light and nutrients between these two groups of benthic organisms is an important factor controlling the development and distribution of coral reefs near the poleward and landward ends of gradients (Johannes *et al.* 1983a, Hatcher 1985).

Complex (often non-linear) interactions amongst water quality parameters (*eg* nutrient concentration, turbidity, temperature) render the comparative approach of observing reef structure and performance along gradients inconclusive. For example, neither Liddell & Ohlhorst (1988) nor Sheppard (1988) were able to unequivocally identify the determinants of declining reef development along geographical axes in the Western Atlantic or Arabian Gulf regions from synoptic comparisons of coral abundance and diversity. Clearly, no single factor controls the transition from coral reef to kelp bed. Rather, the total environment must be considered in terms of its effects on the competitive abilities of the pool of available benthic organisms. Oceanographic conditions exert major, but not exclusive controls, on this environment.

Coastal runoff and its accompanying sedimentation have great potential to modify the influence of boundary currents on reef distribution and development, because of their strongly negative effects on coral growth and survival (reviewed in Birkeland 1988, Hatcher *et al.* 1989). The arid conditions of Western Australia modify the influence of the Leeuwin Current on reef development along the coast to a lesser extent than, for example, the wet coast of east Africa modifies the influence of the Agulhas Current.

Examination of the distribution and structure of coral reefs influenced by the Leeuwin Current reinforces the conclusions drawn above.

Coral Reefs of the Leeuwin Province

Four major and two minor coral reef systems fall under the influence of the Leeuwin Current (Fig.2, Table 1). From north to south they are:

1) The Rowley Shoals,
2) The Dampier Archipelago & adjacent reefs of the Pilbara coast,
3) The Ningaloo reef tract and adjacent reefs,
4) The western islands of Shark Bay,
5) The Houtman Abrolhos reefs and adjacent banks, and
6) The Pocillopora reef at Rottnest Island.

With the probable exception of the Rowley Shoals, all of the Leeuwin reefs were high and dry at the start of the Holocene transgression 10,000 years ago. Their colonization and growth is a geologically recent event.

It is important to be precise about the definition of a coral reef in this context. Isolated coral colonies, or spatially restricted groups of corals, and their associated epi- and infauna extend at least as far south as Cape Naturaliste. They do not form the vertically or horizontally accreting structures of coral framework, infilled and cemented by detritus and algae, which are here defined as coral reefs. It is quite possible that there are other small reef structures fringing the coast between Northwest Cape and Perth (*eg* Point Quobba, just north of Shark Bay, Veron & Marsh 1988) which would meet these criteria, but they have not been described adequately. Knowledge of such reefs would be useful in separating coastal from Leeuwin Current influences on coral reef development.

The four reef systems differ markedly in their physiography, geology and degree of interaction with the Leeuwin Current.

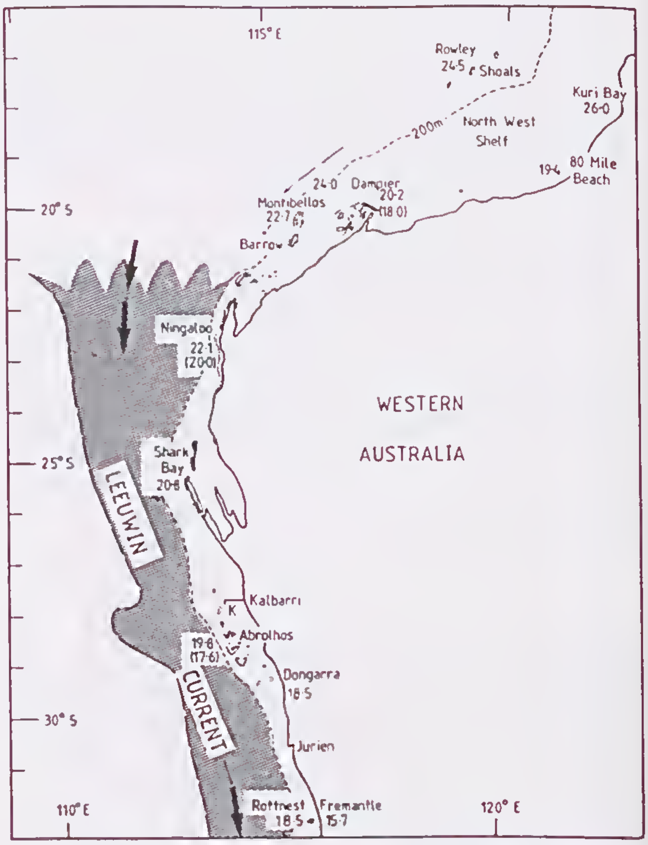

Figure 2 Chart of the coral reefs of Western Australia which are potentially influenced by the Leeuwin Current, showing the 200 m depth contour, the main stream of the Current, and the northern limit of kelp (*Ecklonia*) occurrence (K). Minimum mean monthly sea surface temperatures are shown in °C for reef and coastal locations, with absolute minimum values recorded in brackets (from Veron & Marsh 1988).

Table 1.

A comparison of relevant attributes of coral reefs of Western Australia which potentially fall under the influence of the Leeuwin Current.

Diversity = # genera/# species, N/D = No Data, Extreme lower temperatures in brackets.

Reef system	Reef Type	Lat. °S	Dist. from Coast km	Dist. between Reefs km	Surround Depth m	Dist. from Slope km	Min. mean Temp °C	Water Quality	Best coral Growth	Abundnt Macro-Algae?	Coral Diversity
Rowley Shoals	Atoll?	17	250-300		200-400	0	24.5	Oceanic, Tidal	Slopes & E lagoons	No	52/180
				300							
Dampier Archr.	Fringe	20	5-25		10-20	75-100	20.2 (18.0)	Coastal, Tidal	NW. slopes	Yes	57/216
				120							
Monte-bellos	Fringe	20.3	80-120		30	25-40	22.7	Shelf, Tidal	W. slopes	No	30/66
				10							
Barrow Island	Fringe	20.5	60		25	60	N/D	Shelf & Coastal	W. shore	Yes	15/25
				120							
Ningaloo Tract	Fringe/ Barrier	21-23	0.2-7		15	8-50	22.1 (20.0)	Oceanic & Shelf	Flat & Lagoons	No	54/203
				100							
Shark Bay	Fringe	24-26	0		25	60-80	N/D	Shelf & Coastal	W. shores	N/D	28/82
				250							
Houtman Abrolhos	Plat-form	28-29	45-70		30-40	10-20	19/8 (17.6)	Oceanic & Shelf	E. slopes & Lagoons	Yes	42/184
				330							
Rottnest Island	Fringe	32	20		15-30	20-30	18.5	Shelf & Coastal	S. shore	Yes	16/25

The Rowley Shoals

The Rowley shoals are shelf-slope platform reefs of classic structure and development (Fairbridge 1971). As such, they probably represent a long history of reef growth, with a relatively thick, coral-rich Holocene stratum on the Pleistocene reef basement (Berry 1982). Their position, 700 km northwest of what is generally depicted as the northern limit of the Current at Exmouth (*eg* Pearce & Cresswell 1985), begs the question of their classification as Leeuwin reefs. Currents on the Northwest Shelf, however, exhibit a distinct SW component which is coherent with the Leeuwin Current flow further south (Holloway & Nye 1985), suggesting that this area forms part of the headwaters of the Current. Eastward flowing water from the northern Indian Ocean (and perhaps a southwestward flow from the Timor Sea) undoubtedly bathes the Rowley Shoals as it assembles for its rush south along the shelf slope in the Leeuwin Current.

The Dampier Archipelago & adjacent reefs of the Pilbara coast

A similar generalization applies at least to the outer portions of the Dampier Archipelago and adjacent Lowendal, Monte Bello and Barrow Islands, which occupy the inner, southeast portion of the Northwest Shelf. The coral reefs comprise an extensive array of small, barrier and fringing reefs growing in shallow water adjacent to hundreds of small continental islands (Simpson 1988). They are primarily Holocene structures, resting on non-reefal basements of continental rock. A large range of reef habitats, from high energy, coral covered outer reef slopes to stagnant, depauperate lagoons is the result of this geographic diversity (UNEP/IUCN 1988).

From about February to June the currents on the shelf adjacent to these reefs are predominantly southwest (Mills *et al.* 1986). The source of the water in these currents is unclear, but its quality is strongly influenced by benthic resuspension and runoff from

the adjacent coast (Simpson 1988). Whether it is considered part of the Leeuwin Current or not, much of the water flowing through these reef systems during that period soon joins the Current off Exmouth.

The Ningaloo reef tract and adjacent reefs

The Leeuwin Current is a clearly delineated entity at the Murion Islands off the north end of the Ningaloo reef tract. Australia's largest fringing reef system is separated from the arid coast by only 0.2 to 7 km of shallow lagoon. The best coral reef development occurs in reef passes and within this lagoon. Although the shelf is narrow here, the outer reef slopes are not characterized by rich coral communities extending to great depth, as found, for example at the Rowley Shoals. It appears that the underlying structure of the reef below about 10 m depth is not a Pleistocene reef matrix, but rather a mixture of aeoleanites, calcarenites and tertiary limestones supporting very few corals (May *et al.* 1983, Veron & Marsh 1988, UNEP/IUCN 1988). The Ningaloo Reef tract is likely to be a thin layer of coral matrix built on old coastal features during the Holocene transgression, rather than an ancient coral reef. Perhaps reduced precipitation during the Holocene allowed the reef to grow closer to shore than had been possible during previous interglacial periods.

Having made statements about the structure of Leeuwin reefs, I emphasize that it is impossible to be certain about their underlying composition because no coring has been done. The holes currently being sunk at the Abrolhos (see Collins *et al.* 1991) should fill a major gap in our knowledge.

The pattern of circulation within the Ningaloo reef lagoon ensures rapid exchange with the waters immediately adjacent to the outer reef edge (Hearn *et al.* 1986). There are few oceanographic data from outside the reef, but the proximity of the shelf break (Fig.2) strongly suggests that the Leeuwin Current is the major reservoir for lagoonal exchange.

Shark Bay

Narrow fringing reefs partially line the seaward edges of the islands which form the western boundary of Shark Bay. The islands separate the high salinity water of this large inverse estuary from the shelf waters, and the corals are best developed on their seaward margins (Veron & Marsh 1988). Because there has been little documentation of the biota or physical environment of these reefs, it is difficult to assess the influence of the Leeuwin Current on them. The continental shelf is over 100 km wide at this latitude, however, so the potential influence of the Leeuwin Current is likely to be attenuated.

The Houtman Abrolhos reefs and adjacent banks

On the edge of the shelf between 28 and 29°S latitude lie a series of submerged and emergent reefs which often receive the full force of the Leeuwin Current (Fig.3). While undeniably the products of coral accretion over geological time periods, the Houtman Abrolhos Reefs are unlike any other Australian reef system in morphology and community structure (Saville-Kent 1897, Veron 1986). A Holocene coral veneer is virtually non-existent on the western, that is, seaward portions of the reef platforms. Instead, there grows an unusual mixture of macroalgae of temperate and tropical affinities (Hatcher 1985, Hatcher *et al.* 1987). Yet the relicts of classic spur and groove topography, symptomatic of healthy reef accretion in high energy environments, are evident.

In the eastern portions of the platforms extensive and diverse accumulations of Holocene coral matrix dominate what is clearly a severely eroded Pleistocene reef topography. In places like Turtle Bay in the Wallabi Group, the Pleistocene reef structures are exposed to reveal rich coral sequences (Teichert 1947, Collins *et al.* 1991).

Several shoals and banks are located on the shelf and slope both to the north and south of the Abrolhos (Figs.2 & 3). To what extent these represent extant or extinct coral reef structures is unknown.

The Leeuwin Current rides the slope 10 to 20 km west of the Abrolhos Reefs, and there appears to be a persistent, large scale (100 + km) cyclonic eddy in the current at this latitude (Fig.2). Sporadically, the warm waters of the Current flood the shelf edge around the Abrolhos, while at other times it forms a narrow jet well to the west (Pearce & Griffiths 1991, Pearce *et al.* 1991).

Rottnest Island

The inclusion of Rottnest Island in a classification of coral reefs is debatable. Most corals on this continental island 20 km off the coast near Perth exist as solitary colonies resting on the submerged limestone platforms which surround the Island (Hodgkin *et al.* 1959). In this respect it represents coral communities found on the coast from Jurien Bay, 150 km north of Rottnest Island, to as far south as Cape Naturaliste and Esperance. Pocillopora Reef, on the south coast of Rottnest Island, is a coral reef structure of about 3 m maximum relief which is dominated by the one species, but which supports many other tropical invertebrates and fish. As such, it meets the minimum criteria of the reef definition used here. It is unlikely that the underlying structure is a Pleistocene reef matrix. A relict coral reef of late Pleistocene age outcrops on the south coast of the Island nearby at Fairbridge Bluff (Playford 1988). It appears to represent a thin but extensive sequence of coral matrix now obscured by non-reefal, Holocene deposits, and indicates that conditions suitable for coral reef development here are not restricted to the recent past.

Rottnest Island is not as proximal to the course of the Leeuwin Current as are the Abrolhos Reefs, but the presence of the Current is evident in sea surface

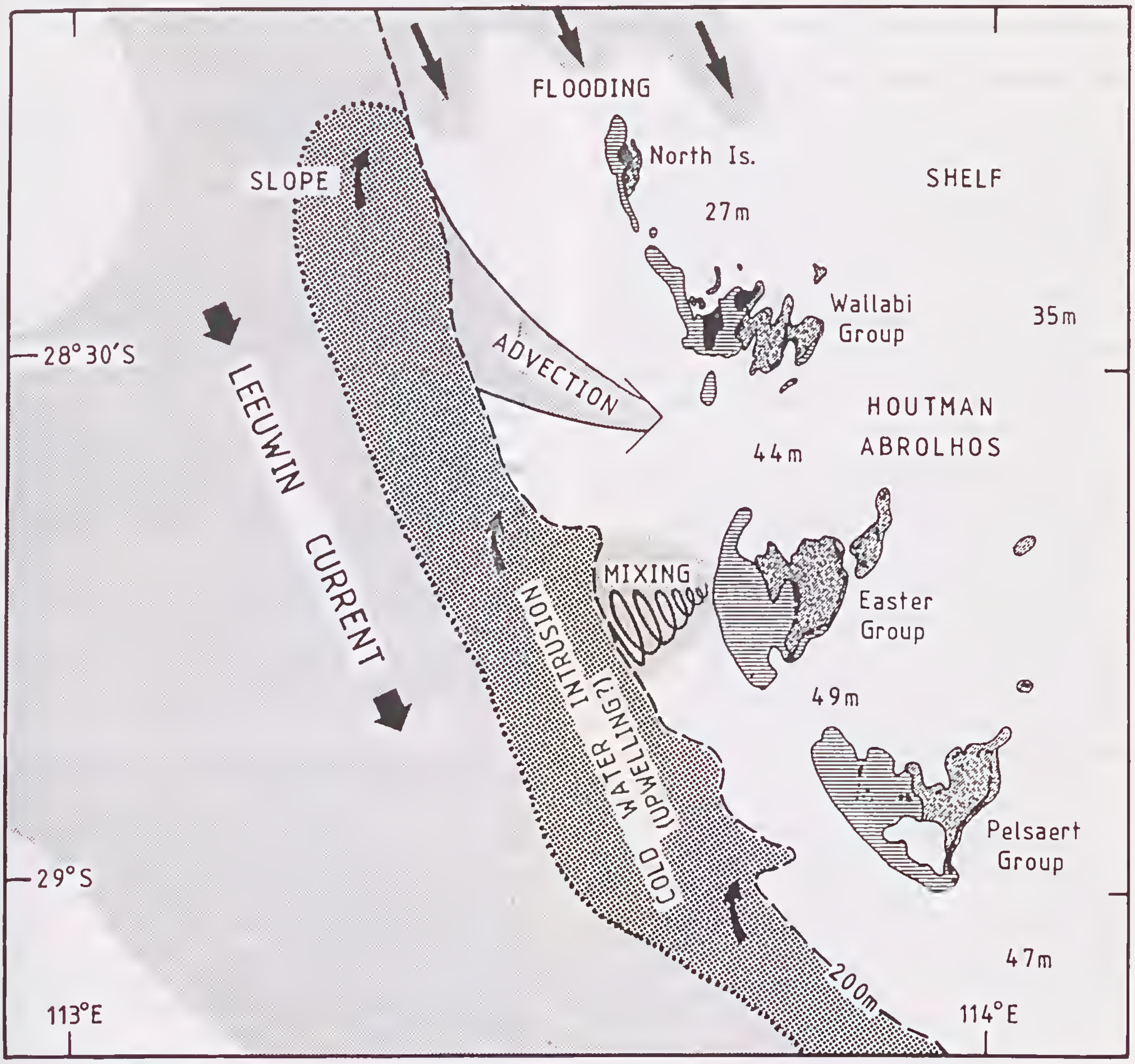

Figure 3 Chart of the Houtman Abrolhos, showing the three major reef platforms (island groups), the 200 m depth contour and representative shelf depths, and generalized circulation features (based on analysis of NOAA-AVHRR imagery, Pearce *et al.* 1991). Areas of subtidal reef dominated by macroalgal communities (horizontal lines) and coral communities (diagonal shading) surround the islands (solid black). Three mechanisms by which Leeuwin Current water (light stipple), and upwelled or intruded water (dark stipple) can influence the reefs on the shelf are depicted.

temperatures and the local hydrography (Pearce *et al.* 1989).

Inter-reef comparisons

Comparison of the salient features of these reef systems (Fig.2, Table 1) reveals several interesting generalizations about the relationship between coral reefs and the Leeuwin Current. With the possible exception of the northern extremity, where temperatures increase shorewards towards Broome, the Leeuwin Current maintains warmer sea surface temperatures at offshore reefs than on the adjacent coast. South of Shark Bay, winter temperatures near the coast often go below 18°C in August or September. The absolute minimum values are generally about 2°C colder (Table 1): for the most part this is a patchy data set, requiring cautious interpretation. I suggest that the offshore and coastal means at the same latitude are significantly different, but that the ranges usually

overlap. The lack of coastal reef development south of Shark Bay suggests either that it is only the mean (rather than the extreme) temperature that matters, or that factors other than temperature are at work.

The reefs of the Leeuwin Province may be divided into offshore and coastal groups, the criterion being distance from the shelf break, rather than distance from the coast. The critical distance appears to be about 50 km from the 200 m depth contour (Table 1). Coastal reefs only occur north of the Abrolhos, and are characterised by more turbid water and greater macroalgal abundance than those offshore. This distinction is most apparent in a comparison between the Monte Bello Islands, which have low macroalgal cover and twice the coral diversity of the reef on nearby Barrow Island, which has abundant macroalgae (UNEP/IUCN 1988).

There is considerable evidence to demonstrate that the presence of macroalgae inhibits coral settlement, growth and survival (Johannes 1975, Crossland 1981, Hatcher 1985). Unlike offshore reefs to the north of Shark Bay, those at the Abrolhos support luxuriant macroalgal communities, including the kelp *Ecklonia radiata* (Hatcher *et al.* 1987), which has its northern coastal limit near Kalbarri (Fig.2). Proximity to the coast, and all it implies in terms of water quality and biotic communities, must thus be seen as another gradient of Leeuwin Current influence, in addition to the more obvious latitudinal cline.

The Role of the Leeuwin Current

Coral reefs are surface phenomena, and as such are particularly influenced by shallow circulations like the Leeuwin Current. Coral reefs are also multidimensional structures which cannot be classified on any single axis. In attempting to interpret the relationship between the Leeuwin Current and its reefs, the multiplicity of factors which interact to control reef structure and development precludes simple cause and effect assumptions in the absence of experimental data. Virtually all of the data available at present are either circumstantial or correlative.

In its simplest guise, the role of the Leeuwin Current in maintaining coral reefs on the coast of Western Australia can be viewed as the flux balance between southern Indian Ocean water derived from the West Wind Drift, and tropical water delivered by the Leeuwin Current. Where mixing is weak and Leeuwin flows dominate, conditions for reef development are good. Where mixing is rapid and Leeuwin flows are diluted and dissipated by their interaction with other water masses, conditions are poor. In this context, one expects to see an attenuation of reef development as one moves away from the centre of the Current (*ie* across the shelf towards the coast or out into the Indian Ocean), and as one moves south and the gradients across which mixing processes occur steepen. It would be nice to have a simple mixing parameter which could be used to quantify the relative dilution of Leeuwin water along these longitudinal and latitudinal axes. Thompson's (1987) scaling model of the Current at shelf scale might be a good place to start.

Several hypotheses can be erected concerning the role of the Leeuwin Current in maintaining coral reefs along the coast of Western Australia. I have listed some of the more obvious ones here:

The first might be termed the "Recruitment Hypothesis":

"Advective delivery of the larvae of reef building organisms in the Leeuwin Current replenishes local populations after local extinctions, and maintains populations of reef organisms at sites where they are not reproductively viable."

Given typical drifter transit times in the Current (Cresswell & Golding 1980), and a maximum distance between any two Leeuwin reef systems of just over 300 km (Table 1), inter-reef transport during the larval stages of most reef-building organisms is entirely feasible (Maxwell & Cresswell 1981).

Two other hypotheses deal with the effect of the Current on water quality in and around offshore and nearshore reef systems. The "Advective Influence Hypothesis":

"Direct advection of Leeuwin Current water maintains elevated temperatures and depressed dissolved nutrient and particulate concentrations which favour the growth of coral reef organisms, and inhibits the growth of macroalgal competitors at offshore sites where the seabed intersects the photic zone and the Current."

The "Mixing Influence Hypothesis":

"Mixing of Leeuwin Current water onto the shelf has a similar effect as advected water masses, but it is attenuated by the quality and quantity of coastal water with which it mixes."

The Advection Hypothesis primarily concerns latitudinal variations in reef development, while the Mixing Hypothesis concerns cross-shelf variation

A fourth hypothesis again concerns water quality for reef development at offshore locations: the "Upwelling Inhibition Hypothesis"

"The Leeuwin Current inhibits wind-driven upwelling of colder, nutrient enriched water on the shelf slope and outer shelf. The degree of inhibition is proportional to the magnitude of the Current in relation to the opposing wind-driven flow."

The degree of upwelling along the coast of Western Australia has been a matter of debate at least since Schott's paper of 1933, and the jury is still out. Certainly it is not a pervasive phenomenon, but even sporadic, local delivery of cold, nutrient-rich water to shallow

reefs can have profound effects on community structure and function.

Processes of upwelling and terrestrial runoff which deliver cold and/or nutrient-rich waters to shallow benthos favour the growth of macroalgae, and have been implicated in the inhibition of reef development. The best examples come from temperature and nutrient proxy records in the skeletons of massive coral colonies collected from currently dead or dying reefs in the eastern Pacific. Increased intensity of coastal upwelling resulting from an equatorward shift in the tradewinds during the little ice age (1500-1850 AD) is implicated in the death of a reef tract on the SW coast of Costa Rica some 150 to 300 years B.P. (Glynn *et al.* 1983). Markedly increased surface concentrations of inorganic nutrients from the Equatorial upwelling occurred during this same period at the Galapagos, suggesting greatly reduced El Niño (Panama Current) flows, and a possible explanation for the scarcity of modern corals at this site (Shen *et al.* 1987, Lea *et al.* 1989, Linn *et al.* 1990). On a more recent time scale, isotopic variations in the thickness and density of growth bands in corals from many locations have been correlated with intra and interannual variations in seawater conditions as influenced by local and global (ENSO) oceanography (*eg* Knutson *et al.* 1972, Smith *et al.* 1979, Boto & Isdale 1985, Barnes & Lough 1989, Hudson *et al.* 1989).

Finally, the dissipation and mixing of Leeuwin Current water as it moves south leads to the "Latitudinal Attenuation Hypothesis":

"All of the effects of the Leeuwin Current are attenuated with latitude, such that a gradient of decreasing diversity, abundance, growth rates and interconnectedness of coral reef communities occurs."

A corollary exists in the compressed gradient towards the coast as Leeuwin water is altered by mixing and terrestrial influences.

The last is not really a testable hypothesis, in that Leeuwin Current effects on reef development are confounded by latitudinal variation which is independent of the Current, such as the latitudinal gradient in solar radiation. It is thus important to identify the mechanisms by which observed gradients in coral reef distribution, structure and function along the Western Australian coast are maintained. Three are obvious.

Mechanisms of Leeuwin Current Influence

A gradient of decreasing species diversity of reef building organisms to the south and east is an obvious feature of Leeuwin reefs (Table 1). It is complemented by an increase in the diversity of competing organisms such as kelp. These changes in community structure provide the simplest explanation for the observed decline in the quantity and quality of reef structures along the Leeuwin gradients. Reefs won't develop in the absence of corals to build framework and associated flora and fauna to cement and infill that framework. If we assume that all shallow areas under the influence of the Current have an equal potential for the survival of recruits, then two mechanisms exist to explain the progressive decrease in the reef-building species pool. Either the species have not reached many potential reef sites in the Leeuwin province from some Indonesian source of radiation, because there has been insufficient time for the advective delivery of critical numbers of larvae, or the larvae have all died *en route*.

The first case is unlikely because the dynamics of the Leeuwin Current favour rapid and direct larval advection, the close proximity of its reefs along stream favour larval advection and "island hopping", and there have been at least 6000 years of relatively stable conditions for dispersal. If there are mechanisms which prevent entrainment of larvae in the Current (*eg* spawning at times of reduced or reversed Current flow), they must be very closely tuned to the Current's dynamics. The only data available suggest that biological mechanisms serve to enhance, rather than inhibit, entrainment of coral larvae (Simpson 1991).

In the second scenario gradients in the physical and biotic environment of the Current cause increased larval mortality due to dispersion, thermal stress and starvation in the south and east of the Current stream. This is a more likely mechanism for producing the observed diversity gradients among Leeuwin reefs, but one for which there is little direct data. At the extreme southern end of Leeuwin reef development at Rottnest Island, the recruitment of *Pocillopora* colonies with genotypes differing from adjacent colonies is very patchy in space and time (Stoddart 1984). The recruitment of tropical fish species to Pocillopora Reef is also a rare event compared to tropical reefs (Hutchins 1991), suggesting that depletion of both larval abundance and diversity down the current is an important phenomenon.

If, on the other hand, we assume that reef-building organisms have equal potential for recruitment to shallow locations within the Leeuwin province, then the observed pattern of reef distribution and development is due to variations in post-recruitment growth and mortality. In this case differences among reefs are due to differences in their local physical, chemical and biotic environments. Observed variation in potentially controlling factors such as reduced sea temperature and increased nutrients, particulates and coral competitors southwards and shorewards are strongly influenced by the Leeuwin Current. Gradients in the marine environment, largely maintained by the Current's flow southwards, provide the most obvious mechanism for maintaining gradients in coral reef development along the Western Australian coast.

A third mechanism is variation in habitat diversity. If we again assume that reef-building organisms have equal potential for delivery to all Leeuwin reef sites

(admittedly unlikely), then differences among reefs may be due simply to variation in the range of habitats available for colonization and suitable for accretion at any given site. Habitat diversity is undoubtedly a major determinant of coral species diversity at the scales of individual reefs (Rosen 1971, Veron 1986). There is no evidence, however, for the consistent geographic variation in habitat diversity at the scale of the Leeuwin Current, which would produce the observed patterns of species diversity (Table 1). Indeed, some of the most southerly sites, such as Rottnest Island and the limestone reefs north of Perth, offer extreme habitat complexity, yet support species-poor coral and coral-associated communities (Hodgkin *et al.* 1959, Marsh 1974).

The mechanisms proposed here are not mutually exclusive. Undoubtedly all three operate to some extent in producing the pattern of reef development within the Leeuwin Province. On the available data, it appears that the Leeuwin Current exerts its major influence by maintaining gradients of temperature, dissolved macronutrients and particulate organics which determine the growth and survival of reef-building organisms in planktonic and benthic stages of their life histories, through both direct physiological effects, and indirect competitive (and predation) effects.

Understanding the influence of the Leeuwin Current on the structure and function of its coral reefs is not simply a question of determining effects on the environmental factors which currently control benthic community structure, growth rates and other parameters of existing reefs, although that is a good place to start. Also required is a knowledge of the geological history of their development, both in terms of changes in the Leeuwin Current itself, and changes in global parameters such as sealevel, surface radiation and source pools of colonizer species. Fortunately, while temporally integrating environmental influences on their development, coral reefs also record many of those environmental signals. Our best clues to the past influence of the Leeuwin Current on coral reef development off Western Australia lie within the calcium carbonate matrix of the coral skeletons themselves. This record is only now being exposed (Collins *et al.* 1991, Pearce *et al.* 1991).

The Houtman Abrolhos - Australia's Galapagos

The Houtman Abrolhos epitomize the anomalous ecological consequences of the Leeuwin Current. Southernmost in the Indian Ocean, the Houtman Abrolhos are coral reef communities at the limits of existence, extending, with the help of the Leeuwin Current, well into a region dominated by macroalgal communities. Northernmost in the South Pacific, the macroalgal communities of the Galapagos are at their limits of existence also, extending well into a region dominated by coral reef communities, with the help of the Peru Current and upwelling of the Equatorial Undercurrent. In both archipelagos, coral and macroalgal communities vie for dominance of the substrata, with the outcome apparently dependent on their local oceanography.

One of the most striking and counter-intuitive aspects of the Abrolhos reefs is the lack of vital coral communities on the most characteristic coral-built structures: the windward reef slopes (Fig.3). Clearly, what used to be actively accreting coral structures are now kelp beds (Wilson & Marsh 1979, Hatcher 1985). When did this transition take place? What was the cause of it? Is it an ongoing process? What is its relationship to the structure and dynamics of the Leeuwin Current?

Analysis of NOAA AVHRR satellite images demonstrates that both direct advection of Leeuwin Current water onto the platforms (shelf flooding and cross-shelf streams), and cross-shelf mixing between Leeuwin & shelf water can influence the Abrolhos (Pearce *et al.* 1991, Fig.3). Whatever the mechanism, the portions of the Abrolhos likely to experience the strongest Leeuwin Current influence are the western reef margins and adjacent lagoons: the areas with the poorest reef communities (Fig.3), and no apparent accretion.

In contrast, the eastern margins and lagoons experience more contact with cooler, nutrient enriched coastal water masses moving north along the shelf under the influence of the prevailing winds (Cresswell *et al.* 1989). Yet these portions of the reefs support the richest coral communities south of Ningaloo (Table 1, Fig.3), high community production and calcification rates (Smith 1981), and obvious vertical and horizontal accretion (Wilson & Marsh 1979, Hatcher 1985, Collins *et al.* 1991, Hatcher, unpublished data).

It is possible that the present distribution of corals within the Abrolhos is related to human activities there (Hatcher *et al.* 1990). Perhaps the distribution reflects differences in wave energy. Many of the robust corals which characterise wave swept reef fronts do not occur at the Abrolhos (Veron & Marsh 1988, Veron pers.comm.): have those species simply not been able to survive the trip? There is no evidence to suggest that corals adapted to high energy environments are less capable of dispersion. The alternative explanation is that conditions for the growth of corals on the exposed portions of the Abrolhos reefs are unsuitable for coral growth and survival.

Experimental results demonstrate that macroalgae are able to outcompete corals for light and space at the Abrolhos, particularly in the absence of intense herbivory (Crossland 1981, Johannes *et al.* 1983a, Hatcher & Rimmer 1985, Hatcher, unpublished data). The nutrient concentrations required to maintain high biomass communities dominated by macroalgae are also known to characterize the lagoons and adjacent waters of the Abrolhos reefs (Johannes *et al.* 1983b, Crossland *et al.* 1984, Hatcher 1985). Indeed, nutrient

concentrations at the Abrolhos are the highest ever recorded in an unpolluted coral reef ecosystem (Crossland 1983), averaging 3 to 12 times the mean values in the centre of the Leeuwin Current stream. The concentration gradient is hypothesized to be largely the result of the decomposition of macroalgae advected into the lagoons from the windward reef slopes (Crossland *et al.* 1984, Hatcher 1983, 1985, unpublished data).

While nutrients are effectively sequestered and recycled by the reef systems of the Abrolhos, the efficiency cannot be perfect. New nutrients necessary to maintain the observed macroalgal growth and concentration gradient must be supplied from outside the reef systems at time scales at least approximating the turnover times of the dominant macroalgae: seasonally to annually. Cross-shelf mixing of coastal waters, enriched by terrestrial inputs (Cresswell *et al.* 1989) is a possible source of new nutrients to the Abrolhos ecosystems, but the distribution of macroalgal communities on the reefs argues against it as the major source.

The satellite images occasionally show tongues of cold water off the western margins of the reefs (Fig.3; Pearce, Hatcher & Wyrwoll, unpublished data). If these represent upwelled water, enriched in nutrients from off reef sources, then they could explain the high biomass of macroalgae (including the kelp *Ecklonia*) at these sites. A temperature logger at 5 m depth on the north end of the Western Reef in the Easter Group (Fig.3) records sporadic, several degree drops in sea temperature lasting 2 to 6 days (Pearce & Hatcher, unpublished data). Without simultaneous nutrient data this is not conclusive evidence of upwelling. It is notable that the upper depth limit of *E. radiata* on the western reef slopes at the Abrolhos occurs at about 5 m, while the most luxuriant growth is from 15 to 45 m. Upwelling (or "uplifting" cf. Rochford 1991) on these reef slopes may rarely reach the sea surface.

The case of *Ecklonia* growing on the fringing coral reefs of the coast in the Gulf of Oman provides a fascinating counterpoint to the Abrolhos situation. There the kelp also does not grow above 5 m depth. It has developed an annual growth strategy which is tuned to the well-documented and highly seasonal monsoon-driven upwelling. The nutrient-needy sporophyte is found only during the upwelling period. For the remainder of the year, the plants survive as microscopic gametophytes, and the benthic community looks like a typical coral reef (Barratt *et al.* 1984). In the Gulf of Oman, upwelling allows the development of kelp beds on coral reefs within the tropics.

The answers to the related questions of the source of nutrients to support macroalgal growth, and the time course of macroalgal versus coral domination of benthic communities at the Abrolhos lie in an improved understanding of the regional oceanography, and of the geological growth history of these reefs. The necessary research is in progress (Pearce *et al.* 1991, Collins *et al.* 1991) and the results will provide the best evidence to date on the role of the Leeuwin Current in the development of coral reefs along the coast of Western Australia.

Conclusion

It was obvious to naturalists of the last century that the regional oceanography of Western Australia controlled the development of reefs along its coast (Saville-Kent 1897). We are now in a position to state the obvious with some authority, and to frame testable hypotheses about the mechanisms of control. The definitive statements, however, must await the next century.

Acknowledgements. I thank W.R. Black for presenting this paper orally, and C.J. Crossland and A.I. Hatcher for providing insightful criticism of the manuscript.

References

Barratt L, Ormond R F G, Campbell A C, Hiscock S, Hogarth P J & Taylor J D 1984 Ecological study of rocky shores on the south coast of Oman. IUCN/UNEP, Cambridge/Geneva, 104 pp.

Barnes D J & Lough J M 1989 The nature of skeletal density banding in scleractinan corals: fine banding and seasonal patterns. J Exp Mar Biol Ecol 126:119-134.

Berry P F (ed) 1982 Report on a preliminary survey of the fauna of the Rowley Shoals by the Western Australian Museum in July 1982. West Aust Museum, Perth, 46pp.

Birkeland C 1988 Geographic comparisons of coral reef community processes. Proc Sixth Int Coral Reef Symp 1:211- 220.

Boto K G & Isdale P 1985 Fluorescent bands in massive corals result from terrestrial fluvic acid inputs to nearshore zone. Nature 315:247-255.

Brown B E & Howard L S 1985 Assessing the effects of "stress" on reef coral. Adv Mar Biol 22:1-63.

Burns T P 1985 Hard coral distribution and cold-water disturbances in South Florida: Variation with depth and location. Coral Reefs 4:117-124.

Coles S L 1988 Limitations in reef coral development in the Arabian Gulf: Temperature or algal competition? Proc Sixth Int Coral Reef Symp 3:211-216.

Coles S L & Fadlallah Y H 1991 Reef coral survival and mortality at low temperatures in the Arabian Gulf: New species-specific lower temperature limits. Coral Reefs 9:231-237.

Collins L B, Wyrwoll K-H & France R E 1991 The Abrolhos carbonate platforms: geological evolution and Leeuwin Current activity. In: The Leeuwin Current: an influence on the coastal climate and marine life of Western Australia. (eds. AF Pearce and DI Walker). J Roy Soc WA 74:47-57.

Cresswell G R, Boland F M, Peterson J L & Wells G S 1989 Continental shelf currents near the Abrolhos Islands, Western Australia. Aust J Mar Freshw Res 40:113-128.

Cresswell G R & Golding T J 1980 Observations of a south-flowing current in the southeastern Indian Ocean. Deep-Sea Res 27A:449-466.

Crossland C J 1981 Seasonal growth of *Acropora* cf. *formosa* and *Pocillopora damicornis* on a high latitude reef (Houtman Abrolhos, Western Australia). Proc Fourth Int Coral Reef Symp 1:663-667.

Crossland C J 1983 Dissolved nutrients in coral reef waters. In: Perspectives on Coral Reefs (ed DJ Barnes), Aust Inst Mar Sci, Townsville. 56-68.

Crossland C J, Hatcher B G, Atkinson M J & Smith S V 1984 Dissolved nutrients of a high latitude coral reef, Houtman Abrolhos Islands, Western Australia. Mar Ecol Prog Ser 14:159-163.

Dana J D 1843 On the temperature limiting the distribution of corals. Am J Sci 45:130-131.

Davies P J & Montaggioni L 1985 Reef growth and sea-level change: the environmental signature. Proc Fifth Int Coral Reef Symp 3:477-511.

Downing N 1985 Coral reef communities in an extreme environment: the northwestern Arabian Gulf. Proc Fifth Int Coral Reef Symp 6:343-348.

Fagerstrom J A 1987 The Evolution of Reef Communities. John Wiley & Sons, New York, 600pp.

Fairbridge R W 1971 Coral Reefs of the Australian Region. In: Landform studies from Australia and New Guinea (eds JN Jennings & JA Mabbutt) ANU Press, Canberra.

Godfrey J S & Ridgway K R 1984 The large-scale environment of the poleward-flowing Leeuwin Current, Western Australia: longshore steric height gradients, wind stresses, and geostrophic flow. J Phys Oceanogr 15:481-495.

Glynn P W, Druffel E R M & Dunbar R B 1983 A dead central American coral reef tract: Possible link with the Little Ice Age. J Mar Res 41:605-637.

Hatcher A I, Wright G D & Hatcher B G 1990 Resolving the conflict between conservation values and extractive use of the Abrolhos coral reefs. Proc Ecol Soc Aust 16:55-70.

Hatcher B G 1983 The role of detritus in the metabolism and secondary production of coral reef ecosystems. In: Proceedings of the Inaugural Great Barrier Reef Conference (eds JT Baker *et al.*), James Cook Univ, Townsville. 317- 325.

Hatcher B G 1985 Ecological Research at the Houtman Abrolhos: High latitude reefs of Western Australia. Proc Fifth Int Coral Reef Symp 6:291-297.

Hatcher B G, Kirkman H & Wood W F 1987 The growth of the kelp *Ecklonia* radiata near the northern limit of its range in Western Australia. Mar Biol 95:63-73.

Hatcher B G, Johannes R E & Robertson A I 1989 Review of research relevant to the conservation of shallow tropical marine ecosystems. Oceanogr Mar Biol Ann Rev 27:337-414.

Hatcher B G & Rimmer D W 1985 The role of grazing in controlling community structure on a high latitude coral reef: Measurements of grazing intensity. Proc Fifth Int Coral Reef Symp, Antenne Museum-EPHE, Moorea, 6:229-236.

Hearn C J, Hatcher B G, Masini R J, Simpson C J 1986 Oceanographic processes on the Ningaloo reef, Western Australia. Centre for Environmental Fluid Dynamics, Univ of West Aust, Perth, Report ED-86-171, 121pp.

Hodgkin E P, Marsh L M & Smith G G 1959 The littoral environment of Rottnest. J R Soc West Aust 42:85-88.

Holloway P E & Nye H C 1985 Leeuwin Current and wind distributions on the southern part of the Australian North West Shelf between January and July 1983. Aust J Mar Freshw Res 36:123-137.

Hudson J H, Powell G V N, Robblee M B & Smith T J 1989 A 107 year-old coral from Florida Bay: Barometer of natural and man-induced catastrophes? Bull Mar Sci 44:283-291.

Hutchins J B 1991 Dispersal of tropical fishes in temperate seas of the southern hemisphere. In: The Leeuwin Current: an influence on the coastal climate and marine life of Western Australia. (eds. AF Pearce and DI Walker). J Roy Soc WA 74:79-84.

Johannes R E 1975 Pollution and degradation of coral reef communities. In: Tropical marine pollution (eds EJF Wood & RE Johannes) Elsevier, Amsterdam, 13-51.

Johannes R E, Wiebe W J, Crossland C J, Rimmer D W & Smith S V 1983a Latitudinal limits of coral reef growth. Mar Ecol Prog Ser 11:105-111.

Johannes R E, Wiebe W J & Crossland C J 1983b Three patterns of nutrient flux in a coral reef community. Mar Ecol Prog Ser 12:131-136.

Knutson D W, Buddemier R W & Smith S V 1972 Coral chronometers-seasonal growth bands in reef corals. Science 177:270-272.

Lea D W, Shen G T & Boyle E A 1989 Coralline barium records temporal variability in equatorial Pacific upwelling. Nature 340:373-376.

Liddell W D & Ohlhorst S L 1988 Comparison of Western Atlantic coral reef communities. Proc Sixth Intl Coral Reef Symp 3:281-286.

Linn L J, Delaney M L & Druffel E R M 1990 Trace metals in contemporary and seventeenth century Galapagos coral: Records of seasonal and annual variations. Geochim Cosmochim Acta 54:387-394.

Macintyre I G & Pilkey O H 1969 Tropical reef corals: tolerance of low temperatures on the North Carolina continental shelf. Science 166:374-375.

Marsh L M 1974 Benthic communities of Limestone reefs off Marmion, Western Australia. M.Sc. Dissertation, The Univ. of Western Australia, 119pp.

Maxwell G J H & Cresswell G R 1981 Dispersal of tropical marine fauna to the Great Australian Bight by the Leeuwin Current. Aust J Mar Freshw Res 32:493-500.

May R F, Lenanton R C J & Berry P F 1983 Ningaloo Marine Park. Report and Recommendations by the Marine Park Working group. National Parks Authority Rept No.1, Perth, 67pp.

Menard H W 1986 Islands. Scientific American Books. New York. 230pp.

Mills D A, Pitt D R & Simpson C J 1986 Summary of current meter data collected from the Dampier Archipelago: 1981-1984. W Aust Dept Conserv Environ Note No.178, Perth, 11pp.

Neumann G & Pierson W J 1966 Principles of Physical Oceanography. Prentice-Hall, New Jersey, 545pp.

Pearce A F 1991 Eastern boundary currents of the southern hemisphere. In: The Leeuwin Current: an influence on the coastal climate and marine life of Western Australia. (eds. A F Pearce and D I Walker). J Roy Soc W A 74:35-45.

Pearce A F & Cresswell G 1985 Ocean circulation off Western Australia and the Leeuwin Current. CSIRO Div Oceanogr Info Sheet No. 16-3, 4pp.

Pearce A F & Griffiths R W 1991 The mesoscale structure of the Leeuwin Current. J Geophys Res C96: 16739-16757.

Pearce A F, Prata A J & Manning C R 1989 Comparison of NOAA/AVHRR-2 sea-surface temperatures with surface measurements in coastal waters. Int J Remote Sensing 10:37- 52.

Pearce A F, Hatcher B G & Wyrwoll K-H 1991. Using satellite imagery to interpret the growth history and paleoceanography of the Houtman Abrolhos reefs: patterns of the Leeuwin Current around the Abrolhos. CSIRO/UWA Collaborative Research Grant - Final Report, 20pp.

Playford P E 1988 Guidebook to the Geology of Rottnest Island. Geol Soc Aust, Perth, 67pp.

Roberts H H, Roberts L J, Walker N D, Hudson J H 1982 Cold water stress in Florida Bay and Northern Bahamas: A product of winter cold-air outbreaks. J Sediment Petrol 52:145-155.

Rochford D J 1991 'Upwelling': does it need a stricter definition? Aust J Mar Freshw Res 42:45-46.

Rosen B R 1971 The distribution of reef coral genera in the Indian Ocean. Symp Zool Soc London 28:263-299.

Saville-Kent W 1897 The naturalist in Australia. Chapman & Hall, London, 302pp.

Schott G 1933 Upwelling off Western Australia? Yes or No? (In German) Ann d Hydr usw 61:225-233.

Sheppard C R C 1988 Similar trends, different causes: responses of corals to stressed environments in Arabian seas. In: Proc Sixth Intl Coral Reef Symp (eds Choat *et al.*) James Cook Univ Townsville, 3:297-302.

Shen G T, Boyle E A & Lea D W 1987 Cadmium in corals as a tracer of historical upwelling and industrial fallout. Nature 328:794-796.

Shinn E A 1976 Coral reef recovery in Florida and the Persian Gulf. Env Geol 1:241-254.

Simpson C J 1988 Ecology of Scleractinian corals in the Dampier Archipelago, Western Australia. W Aust Environ Protect Auth Tech Ser No. 23, Perth, 238pp.

Simpson C J 1991 Mass spawning of corals on Western Australian reefs and comparisons with the Great Barrier Reef. In: The Leeuwin Current: an influence on the coastal climate and marine life of Western Australia. (eds. AF Pearce and DI Walker). J Roy Soc WA 74:85-91.

Smith S V 1981 The Houtman Abrolhos Islands: carbon metabolism of coral reefs at high latitude. Limnol Oceanogr 26:612-621.

Smith S V, Buddemeier R W, Redalje R C & Houck J E 1979 Strontium-Calcium thermometry in coral skeletons. Science 204:404-407.

Stoddart J A 1984 Genetic differentiation amongst populations of the coral *Pocillopora damicornis* off southwestern Australia. Coral Reefs 3:149-156.

Teichert C 1947 Contributions to the geology of the Houtman's Abrolhos, Western Australia. Proc Linn Soc NSW 71:145-196.

Thompson R O R Y 1987 Continental-shelf-scale model of the Leeuwin Current. J Mar Res 45:813-827.

Thompson R O R Y & Veronis G 1982 A poleward boundary current off Western Australia. Aust J Mar Freshw Res 34:173-185.

Tribble G W & Randall R H 1986 A description of the high-latitude shallow water coral communities of Miyake-jima, Japan. Coral Reefs 4:151-159.

UNEP/IUCN 1988 Australia, Western. In: Coral Reefs of the World. Volume 2: Indian Ocean, Red Sea and Gulf. UNEP Regional Seas Directories & Bibliographies. IUCN, Gland, Switzerland & Cambridge, UK/UNEP, Nairobi, Kenya. 389pp.

Veron J E N 1986 Corals of Australia and the Indo-Pacific. Angus & Robertson, Sydney, 644pp.

Veron J E N & Marsh L M 1988 Hermatypic corals of Western Australia. Rec W Aust Mus Supplt No.29, Perth, 136pp.

Wells J W 1957 Coral Reefs. Geol Soc Am Mem 67:609-631.

Wilson B R & Marsh L M 1979 Coral reef communities at the Houtman Abrolhos, Western Australia, in a zone of biogeographic overlap. Proc Int Symp Mar Biogeog South Hemisphere, NZ DSIR Info Ser 137, pp.259-278.